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Environmental factors and lumbricid associations in southern Sweden

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With 14 figures

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1. Introduction

A previous study (Nordström and Rundgren 1973) showed that four types of lumbricid associations could be distinguished in certain specified biotopes in southern Sweden. They were delimited by dominance values according to Renkonen (1938). They were distinctly separated regarding biomass, abundance and numbers of species.

The composition of these associations in terms of abundance as well as of biomass, is a result of several co-acting environmental factors. Some of these, in earlier studies pointed out as important, were studied at the same time as the associations were analysed.

2. Study area and biotopes

The Vomb Depression is situated ca. 20 km E of Lund, in the province Skåne, southern Sweden. The soils are mainly glacifluvial deposits but also moraine with high clay content (the Baltic moraine) occur (Nordström and Rundgren 1973, fig. 1). In some areas peat soils are found.

Skåne is situated on the border between a boreal and a more temperate climate (Ångström 1958). The vegetation of the study area reflects the agricultural history of great parts of Sweden. A more or less intensive farming has given way to extensive cattle grazing and on poor soils spruce and pine are planted.

In this vegetationally heterogeneous area 20 biotopes were chosen for study. Due to a radical alteration one biotope had to be omitted. The biotopes varied as concerns agri-cultural history, edaphic factors and present vegetation (for details see Nordström and Rundgren 1973).

Loc. 1. Spruce plantation. 12-year-old trees on former arable land. The field layer still dense.
Loc. 2. Spruce plantation. 25-year-old trees. No field layer.
Loc. 3. Spruce plantation. 45-year-old trees. Sparse field layer in openings.
Loc. 4. Beech wood. Ca. 100 years old. Vernal and summer aspect well-developed.
Loc. 5. Alder-pine wood. Dense shrub and field layers.
Loc. 6. Abondoned grassland. Grazed until 1948. Close to and influenced by Lake Krankesjön.
Loc. 7. Permenent pasture. Cultivated until 1963. After three years in fallow, grazed during the sampling period.
Loc. 8. Pine plantation. 12-year-old trees. No field layer. Pine trees planted in quadrats (8a) separated from each other by 5 m-wide strips of birch (8b). In the birch part a dense field layer dominated by grasses.
Loc. 9. Alder-birch wood. Dense shrub layer, field layer sparse.
Loc. 10. Tall herb meadow. Dense field layer consisting of *Anthriscus sylvestris* (L.) Hoffm., *Circium oleraceum* (L.) Scop., *Geum rivale* L. and *Urtica dioica* L.
Loc. 11. Pine plantation. 25-year-old trees on a former cultivated land. No field layer.
Loc. 12. Elm-ash wood. Mixed, unevenly aged wood with a species-rich field layer, the floral communities of which vary due to spatial variations of the soil moisture regime.
Loc. 13. Juniperus pasture. A land formed by selective grazing.
Loc. 15. Elm-ash wood. Mixed, unevenly aged wood with dense shrub and field layers.
Loc. 16. Spruce plantation. 40-year-old trees. No field layer.
Loc. 17. Beech wood. The vernal aspect of the field layer covering more than the summer aspect.
Loc. 18. Elm wood. Alder trees on both sides of a brook. Tall herbs in a dense field layer.

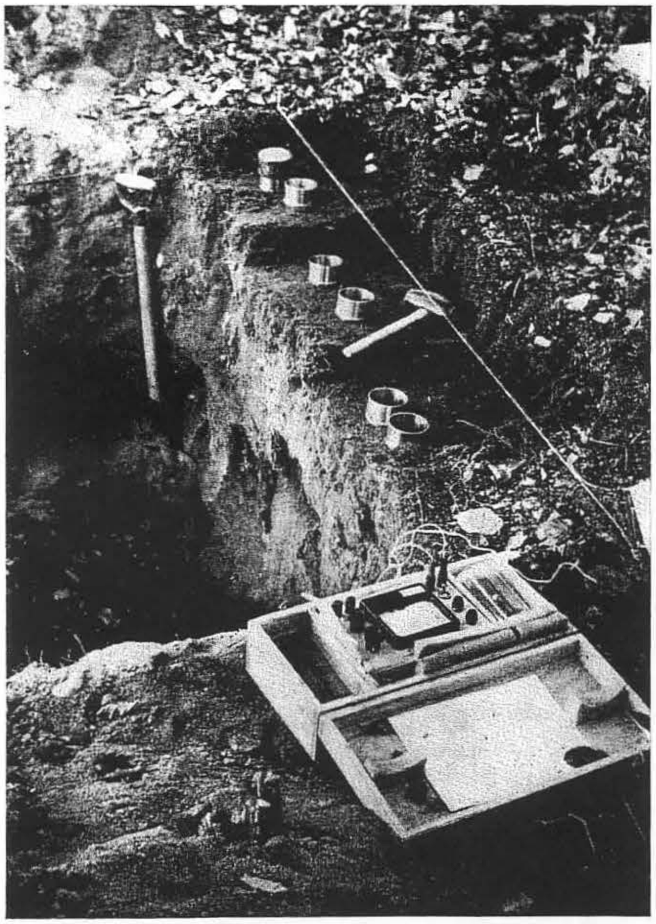

Fig. 1. Soil sampling in beech wood (loc. 4). Samples were taken from successive 5- or 10-cm levels by means of steel cylinders.

Loc. 19. Corynephorus heath. Dominated by grasses (*Corynephorus canescens* (L.) BEAUV., *Agrostis canina* L. and *Aira praecox* L.).
Loc. 20. Alder wood. At the shore of Lake Krankesjön. Strong variations of the soil moisture regime.

3. Methods

3.1. Earthworm sampling

The formaldehyde method was used according to RAW (1959). Sampled squares were 0.5 m². The biotopes were studied during September–November 1966 (the choice of sampling period was discussed by NORDSTRÖM and RUNDGREN 1973). In five biotopes (locs 3, 4, 6, 7, 12) 32 samples/biotope were taken. The other biotopes were sampled 12 times each.

Specimens were killed and fixed in 50% ethanol and preserved in 80% ethanol. Biomass was defined as the weight of the worms after preservation for 3–4 months and after drying for 1 min on filter paper at room temperature.

The nomenclature follows GERARD (1964). Names of subspecies are omitted for *Dendrobaena rubida* (SAV.).

The sampling results are given in table 1 (see also NORDSTRÖM and RUNDGREN 1973).

3.2. Soil properties

Field methods. In every biotope studied a profile was dug down to 100 cm depth. Horizons were distinguished and measured. The occurrence of stones, roots, fissures and earthworm burrows were recorded.

Table 1 Biomass and numbers of earthworms per m² in studied biotopes in Sept.—Nov. 1966. For figures of S. E. see NORDSTRÖM and RUNDGREN (1973, table 1). + = found on some occasion during Nov. 1965 — Jan. 1967

Locality	Number of samples	Biomass (g/m²)	Total abundance (ind/m²)	*Octolasion lacteum* ÖRLEY	*Lumbricus rubellus* HOFFM.	*Dendrobaena rubida* (SAV.)	*Dendrobaena octaedra* (SAV.)	*Lumbricus terrestris* L.	*Allolobophora caliginosa* (SAV.)	*Allolobophora longa* UDE	*Allolobophora rosea* (SAV.)	*Lumbricus castneus* (SAV.)	*Allolobophora chlorotica* (SAV.)	*Eiseniella tetraedra* (SAV.)	*Lumbricus festivus* (SAV.)	*Octolasion cyaneum* (SAV.)
1 Spruce plantation	12	0.68	9.8	—	0.7	3.3	5.8									
2 Spruce plantation	12	0.72	7.0	—	—	0.2	6.8									
3 Spruce plantation	32	3.18	31.6	—	1.7	2.9	27.0									
16 Spruce plantation	12	1.83	33.1	—	+	2.0	30.8	—	0.3							
5 Alder-pine wood	12	2.30	19.4	—	1.7	3.5	14.2	—	—							
8 Pine plantation	12	5.72	28.2	—	—	0.2	22.8	3.7	1.5							
11 Pine plantation	12	10.31	105.3	—	19.5	5.0	80.3	—	0.5							
6 Abandoned grassland	32	6.85	32.5	0.3	6.2	3.4	10.8	0.3	11.5	+						
10 Tall herb meadow	12	19.14	45.2	—	5.9	2.8	17.0	11.7	—	—	1.0	—	6.8			
9 Alder-birch wood	12	20.81	57.8	0.7	18.4	8.8	14.0	9.2	—	—	3.0	0.2	3.5			
20 Alder wood	12	20.82	60.8	—	8.2	0.5	28.5	—	8.8	1.0	1.8	2.2	1.3	0.3	8.2	
4 Beech wood	32	12.39	67.4	—	21.8	8.0	15.6	—	18.8	—	0.8	2.4				
17 Beech wood	12	25.60	89.8	—	13.8	5.8	21.8	7.2	22.9	1.5	7.3	9.5				
13 Juniperus pasture	12	15.48	28.8	—	2.7	—	1.8	6.0	12.6	2.0	1.7	0.5	1.5			
12 Elm-ash wood	32	89.28	208.7	0.6	+	0.1	2.3	59.4	77.4	22.8	24.5	15.3	6.3			
15 Elm-ash wood	12	63.20	121.8	—	8.5	1.5	4.5	40.6	36.7	5.8	4.2	16.2	—			3.8
18 Elm wood	12	78.63	226.5	0.3	46.8	1.5	4.0	15.5	46.5	20.0	50.7	37.8	3.2	0.2		
7 Permanent pasture	32	59.35	109.1	+	—	—	—	50.1	19.7	13.7	22.6	—	3.0			
19 Corynephorus heath	12	3.50	9.5						7.5	2.0						

Five samples were taken from each successive 5- or 10-cm level down to 100 cm by means of steel cylinders, 192.5 and 385.0 cm^3 in volume (fig. 1). The choice of the cylinder height depended on the thickness of the soil horizon in question. Two of these samples were used intact for determinations of soil moisture characteristics (pF 0.4/0.7, pF 2.0, pF 7.0), porosity, permeability but also to mechanical composition. The other samples were transferred to plastic bags and determinations of pF 3.2, pF 4.2, bulk density, organic matter and *p*H were performed on these disturbed soil samples.

Textural composition. The analysis of the fine earth (defined as the part of the soil with particle-size < 2 mm) was done according to GANDAHL (1952). The skeleton fractions (> 2 mm) were determined by sieving air-dried soil. The nomenclature of soil texture classes are according to ATTERBERG.

Organic matter. Loss on ignition was determined at 550 °C on soil dried to constant weight at 105 °C. Values obtained were expressed in weight percentage. Corrections for weight losses due to constituent water was performed according to EKSTRÖM (1927).

Porosity and pores. The porosity of soil in undisturbed stratification was determined according to ANDERSSON (1955). From pF-curves the volumes of structurally dependent pores ($> 2\,\mu$m) and of coarse pores ($> 200\,\mu$m) were calculated (see ODÉN 1957).

Water permeability. Permeability of water(k) was determined by permeameter according to ANDERSSON (1955). The total vertical permeability (k_v) was calculated (ANDERSSON 1953 b).

The determination of the k-value was performed after the determination of the pF-value 2.0. A suction of 0.1 atm was enough to give irreversible deformations to cores of peat soils. The method used is therefore not applicable to organic soils and figures of those are not given.

*p*H. Determinations were performed on fresh soil, 3–4 hr after sampling. Drying in air causes changes in *p*H values (SJÖRS 1961). *p*H was determined electrometrically on fine earth (*p*H-meter type Radiometer pHM 22) in extracts of water. Volume proportion soil : water was 1 : 1.

As the *p*H differences between two adjacent points in the same horizon may be important, especially in F (A_{01}) and H (A_{02}) horizons (VAN GROENEWOUD 1961) the *p*H analysis were performed on samples homogenized by sieving.

Soil moisture characteristics. Soil moisture characteristics are described according to ANDERSSON and ERICSON (1963). Determinations of the pF-values 0.4/0.7, 2.0, 3.2, 4.2, and 7.0 were performed according to NIHLGÅRD (1971). pF-curves were constructed.

3.3. Soil moisture regime

Soil moisture was determined gravimetrically at 105 °C. Samples were taken once a week (locs 3, 4, 6, 7, 12) or every second week (remaining locs) from November 1965 to January 1967. On every sampling occasion two soil cores were taken with a steel-auger from each of the layers 0–5, 5–10, 15–20, 30–35 and 45–50 cm. Mean values were converted to volume percentage and then to pF-values.

The water table was recorded when found above –100 cm.

3.4. Soil temperature

Soil temperatures were measured on four depth (–1, –5, –20, and –50 cm) by thermistors (Hafo type B5-2200-2700-m), read by Wheatstone bridge (type Normameter). Readings were made once a week from November 1965 to January 1967 between 1200 and 1400 hr, when the daily maximum temperature usually occurs in soil surface.

The depth of the tjaele was recorded. As a result of prolonged sub-zero temperatures, the soil water freezes to varying depths. This condition, which is of more-or-less annual occurrence in southern Sweden, is referred to here as tjaele (Sw. tjäle, see also STAMP 1961).

3.5. Weather data and snow depth

From the meteorological stations in LUND and BJÖRKA (10 km SE of the study area) air temperature and precipitation data were obtained. The snow depth of the biotopes was recorded once a week during winter seasons. The mean value of three measurements was calculated.

3.6. Statistical analysis

Surface-living, intermediary, and deep-burrowing species (NORDSTRÖM and RUNDGREN 1973) were correlated by using Pearson's coefficient to values from the 0–5 cm layer, mean values from the 0–20 cm and 0–60 cm layers respectively. Mean differences were tested by Student's t-test.

4. Climatic conditions

The meteorological stations LUND and BJÖRKA are situated in an area of similar air temperatures and precipitation (see ÅNGSTRÖM 1958). Mean monthly air temperature and precipitation during the period studied was compared to mean values for the period 1901–1930 (fig. 2).

From the beginning of November 1965 through April 1966 there was a strong temperature deficit (fig. 2). The period with an air temperature < 3 °C, the limit of the growth period, was 5.5 months instead of normally 4 months. The rest of 1966 the air temperature was normal.

The precipitation during 1966 was greater than normal. Deficits compared with 1901—1930 occurred only in July and October. Large amounts of precipitation during a 2-day period were rare (fig. 8).

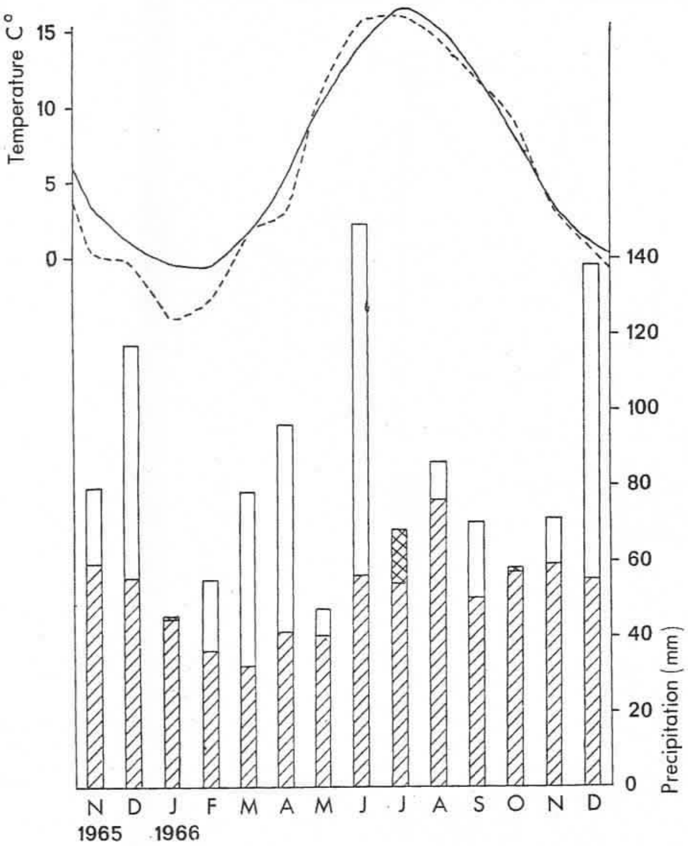

Fig. 2. Air temperature and precipitation in the Vomb area during Nov. 1965 — Dec. 1966 compared to mean values (from Ångström 1958) for the period 1901—1930. Unbroken line = mean monthly air temperature at Lund 1901—1930, broken line = mean weekly air temperature at Björka, diagonally hatched column = mean monthly precipitation at Lund 1901—1930, blank = precipitation surplus at Björka, cross-hatched = precipitation deficit at Björka.

5. Results and discussion

5.1. Soil texture

The texture is of great importance for chemical and physical processes in the soil. Because of their colloidal properties clay particles may indirectly affect soil organisms. The influence of clay content on earthworms was discussed by Kollmannsperger (1934) and Guild (1948).

Four biotopes had organic soils (locs 5, 9, 10, 20) (table 2). On the basis of the clay content of fine earth from 50 cm depth, the biotopes with mineral soils could be divided in three groups:

1. Soils with a clay content of 0—5 % (locs 1, 2, 3, 4, 6, 8, 11, 19). Dominating fractions were sand and fine sand (fig. 3).

2. Soils with a clay content of 5–15 % (locs 12, 13, 18). The silt and fine sand fractions amount to ca. 50 % (fig. 3).
3. Soils with a clay content of 15–25 % (locs 7, 15, 16, 17) (fig. 3).

Mineral soils with low clay content are typical for the glacifluvial deposits of the Vomb Depression, while a high clay content is usually associated with the Baltic moraine. With

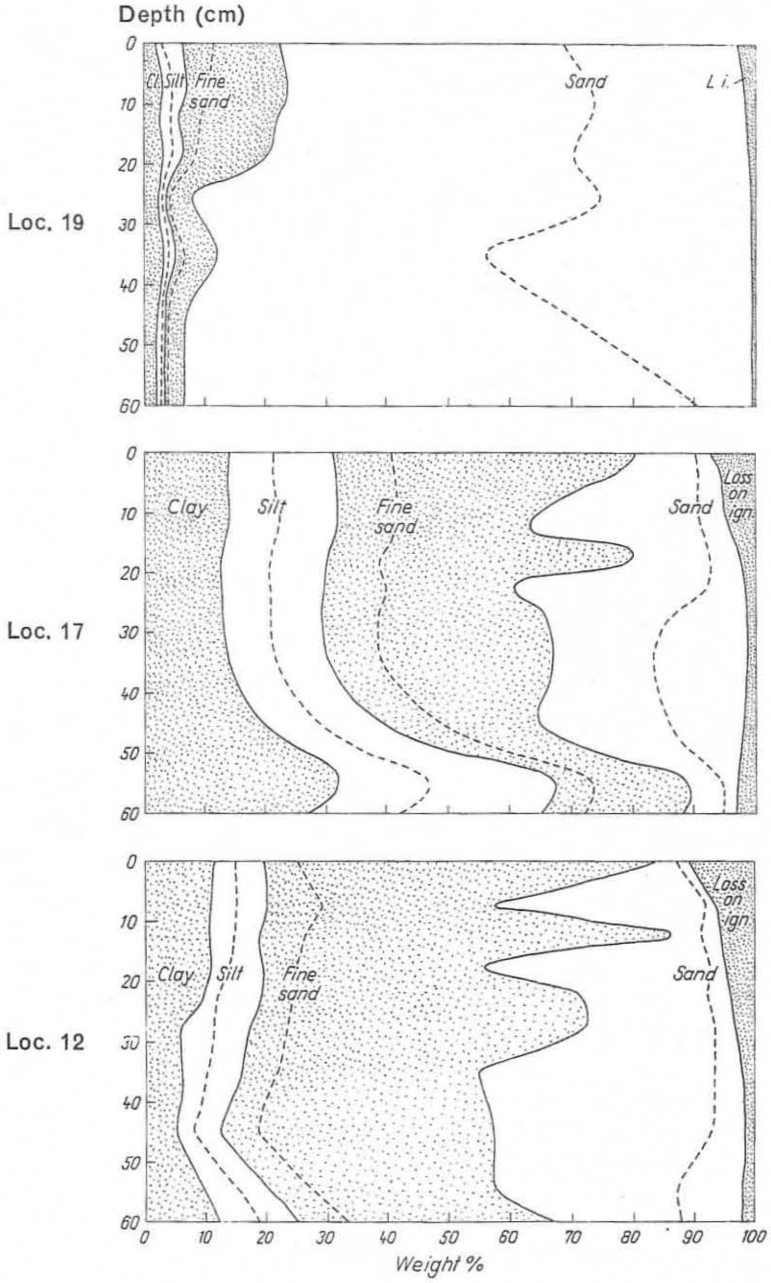

Fig. 3. Mechanical composition of fine earth (< 2 mm) and loss on ignition in Corynephorus heath (loc. 19), elm-ash wood (loc. 12), and beech wood (loc. 17). Only main classes are given, further division according to Atterberg is indicated.

one exception skeleton fractions could be neglected in the soils studied. In the elm wood (loc. 18) on a former impoundment stones and boulders occurred in the layer 20–50 cm.

A positive significant correlation was found between clay content (0–60 cm) and total abundance of earthworms ($r = 0.58$; $0.01 > P > 0.001$). The 25-year-old pine plantation (loc. 11) had a high abundance of lumbricids but a low clay content. In the Juniperus pasture (loc. 13) and the spruce plantation (loc. 16) the clay content was high but the abundance low.

There was no significant correlation between clay content (0–5 cm) and abundance of all surface-living species ($r = 0.11$), except for *L. castaneus* ($r = 0.72$; $P < 0.001$). This species was abundant in deciduous woods with a high clay content (locs 12, 15, 18).

No significant correlation was found between clay content (0–20 cm) and the abundance of *L. rubellus* ($r = 0.35$). This species had its highest abundance in the elm wood (loc. 18), the biotope with the highest clay content (0–20 cm). High values were, however, also obtained in organic soils (loc. 9) and in mineral soils with low clay content (locs 4, 11).

The abundance of deep-burrowing species increased at higher clay contents (0–60 cm) ($r = 0.57$; $0.05 > P > 0.01$) (fig. 4). However, these species were almost entirely absent from the spruce plantation (loc. 16) in spite of high clay content present. The correlations between clay content (0–60 cm) and abundance of the various deep-burrowing species were also significant. The correlation coefficients were 0.57, 0.54, 0.53, and 0.48 for *A. rosea*, *A. caliginosa*, *A. longa*, and *L. terrestris* respectively (all $0.05 > P > 0.01$).

The number of species increased at higher clay contents, but the correlation was not significant ($r = 0.40$).

A relation between high clay content and total abundance was pointed out by KOLLMANNSPERGER (1934). STÖCKLI (1928) was, however, of the opinion that no relation existed. His study was built on wormcast production not on total abundance. KOLLMANNSPERGER (1934) found that lumbricids were absent from pure sandy soils. In the present study associations with six to seven species and 33–67 individuals/m² were found in the beech wood (loc. 4) and in the abandoned grassland (loc. 6), where sand and fine sand fractions constituted 80–90 % (NORDSTRÖM and RUNDGREN 1973). Lumbricids also occurred in the Corynephorus heath (loc. 19) with the same fractions amounting to 92 %. The association was, however, species-poor and had a low abundance.

Dendrobaena spp., *L. castaneus* and to a certain degree *L. rubellus* were concentrated to the superficial organic horizons (litter and mor) (see also NORDSTRÖM and RUNDGREN 1973). Except for *L. castaneus* they were independent of the textural composition of the underlying mineral horizons. In the deciduous woods where *L. castaneus* was numerous, the thickness of the A_{00} horizon had a strong yearly variation (NORDSTRÖM and RUNDGREN 1973). The clay content of A_1 directly or indirectly influenced the abundance of this species.

GUILD (1948) showed that *A. caliginosa*, *A. longa* and to a certain degree *L. terrestris* were more numerous in loamy soils than in gravelly sand. In soils of heavier clay the numbers of these species were lower. In the present study a high clay content had no negative effect on the abundance of these species.

The clay content was of no importance for the distribution of the various species. All species had a wide amplitude with regard to soil texture. Disregarding *E. tetraedra*, *O. cyaneum* and *L. festivus* which occurred sporadically, the remaining ten species were found in mineral soils with a clay content varying from 0 to 20 % and in organic soils. KOLLMANNSPERGER (1934) considered *O. lacteum* to be an exclusive "clay-species". In the present study this species occurred in mineral soils with a clay content of 5 to 18 % as well as in organic soils.

The collodial properties of clay influence among other things soil water retention and cation exchange capacity. A high clay content in the study area is associated with the Baltic moraine which is rich in basic material, and consequently has high *p*H values. The correlations found between clay content and lumbricid abundance are probably of a secondary order, clay being connected with other environmental factors directly influencing the lumbricid associations.

Table 2 Clay content, organic matter, pore volume, water permeability, and pH in studied biotopes in the Vomb Depression

Locality	Clay content (wt-%)			Organic matter (wt-%)				Porosity (vol-%)	
	0–5 cm	0–20 cm	0–60 cm	0–5 cm	0–20 cm	0–60 cm	20–60 cm	0–5 cm	0–20 cm
1 Spruce plantation	5.0	5.1	4.3	10.1	10.2	4.4	1.4	71	66
2 Spruce plantation	4.1	5.3	4.8	8.2	3.5	1.9	1.1	58	50
3 Spruce plantation	2.3	2.7	2.9	35.3	10.7	4.2	1.0	60	51
16 Spruce plantation	12.9	12.9	14.6	32.1	11.6	5.1	1.8	73	56
5 Alder-pine wood	—	—	—	88.3	86.6	89.1	90.8	85	82
8 Pine plantation	5.2	5.3	5.0	3.3	1.8	1.7	1.1	53	49
11 Pine plantation	4.9	5.3	4.7	3.6	1.5	1.2	0.9	53	47
6 Abandoned grassland	7.2	7.3	4.8	14.1	11.6	5.3	2.2	69	67
10 Tall herb meadow	—	—	—	74.9	74.5	74.8	73.3	75	68
9 Alder-birch wood	—	—	—	59.1	56.0	74.9	83.0	75	68
20 Alder wood	—	—	—	56.2	36.6	41.1	44.1	74	65
4 Beech wood	2.8	2.4	2.5	5.9	3.1	2.3	1.0	58	52
17 Beech wood	14.4	14.1	17.8	5.6	4.2	2.8	2.2	54	49
13 Juniperus pasture	8.9	9.4	7.0	9.7	6.4	3.2	1.7	69	53
12 Elm-ash wood	11.7	11.4	9.0	9.2	6.2	3.5	2.1	71	60
15 Elm-ash wood	18.5	17.2	17.5	6.7	5.9	3.8	2.8	53	52
18 Elm wood	19.4	21.0	17.9	10.9	9.4	5.7	3.9	60	60
7 Permanent pasture	11.6	10.8	13.7	9.0	7.0	4.6	3.4	52	48
19 Corynephorus heath	2.3	2.8	2.6	2.3	1.8	1.1	0.8	61	41

Locality	Porosity (vol-%)		Volume of pores (%) 20–60 cm		Water permeability k_v (cm/hr)		pH (H_2O)		
	0–60 cm	20–60 cm	2–2000 μm	200–2000 μm	0–20 cm	0–60 cm	0–5 cm	0–20 cm	0–60 cm
1 Spruce plantation	51	43	30	13	17	23	3,6	3.4	4.1
2 Spruce plantation	45	43	32	14	13	19	3.7	3.7	4.1
3 Spruce plantation	47	45	27	14	17	26	3.9	3.9	4.0
16 Spruce plantation	43	36	13	5	16	2.9	4.3	4.0	4.5
5 Alder-pine wood	83	84	36	3	—	—	4.2	4.2	4.4
8 Pine plantation	44	42	31	13	16	13	3.6	3.6	3.7
11 Pine plantation	46	45	35	16	12	11	3.4	3.3	3.5
6 Abandoned grassland	51	43	33	12	131	90	5.3	5.5	6.6
10 Tall herb meadow	74	77	34	3	—	—	5.5	5.2	5.5
9 Alder-birch wood	78	83	46	6	—	—	5.3	5.4	5.1
20 Alder wood	70	73	44	7	—	—	4.3	4.3	4.2
4 Beech wood	47	44	25	13	52	64	4.1	4.1	4.2
17 Beech wood	42	39	13	5	11	1.4	5.3	5.0	4.9
13 Juniperus pasture	46	42	28	10	10	6	4.9	5.0	4.5
12 Elm-ash wood	49	46	23	8	19	0.8	5.5	5.4	5.7
15 Elm-ash wood	44	40	14	5	9	0.5	6.6	6.3	6.6
18 Elm wood	53	49	18	6	25	28	6.0	5.8	6.3
7 Permanent pasture	47	45	16	5	9	1.3	6.4	6.5	6.2
19 Corynephorus heath	39	38	28	14	4	7	5.5	5.7	6.1

5.2. Organic matter

Loss on ignition may be used as an approximate value of the amount of organic matter (see JACKSON 1958) although conversion factors should be used (HOWARD 1966). JULIN (1948), ZUCK (1952) and BOYD (1957) used the loss on ignition in their discussions concerning the influence of organic matter on earthworms.

Four biotopes had organic soils (locs 5, 9, 10, 20) and organic matter varied between 40–90 % in the layer 0–60 cm (table 2). Lowest values were recorded in the alder wood (loc. 20) where films of alluvial fine sand were found. Low values were measured in sand-dominated soils, while soils built up by the Baltic moraine were characterized by higher values. Old spruce plantations (locs 3, 16) had well-developed A_0 horizons and large amounts of organic matter (0–5 cm).

In biotopes on organic soils surface-living species dominated, but deep-burrowing species also occurred except in the alder-pine wood (loc. 5). The amount of organic matter (0–60 cm) in the mineral soils was not significantly correlated to species number ($r = 0.44$) or to earthworm abundance ($r = 0.30$). No significant correlations were found between amount of organic matter and abundance of surface-living species ($r = 0.04$) or deep-burrowing species ($r = 0.38$).

The correlation between organic matter (20–60 cm) and abundance of deep-burrowing species was significant and positive ($r = 0.73$; $0.01 > P > 0.001$) (fig. 4) as was that between organic matter (20–60 cm) and the separate species *L. terrestris* ($r = 0.61$), *A. caliginosa* ($r = 0.59$) (both $5 > P > 0.01$), *A. longa* ($r = 0.71$; $0.01 > P > 0.001$) and *A. rosea* ($r = 0.80$; $P < 0.001$).

Plant litter and other organic matter are sources of food for lumbricids and, as humus, are important for the physical and chemical properties of the soil. The structure and the function of organic matter are not comparable in organic and mineral soils. There was, however, no great difference between these two main types of soil as to species numbers. In the organic soils 12 out of 13 species were found. Organic soils favour associations dominated by surface-living species. The occurrence of deep-burrowing species in the alder-birch wood (loc. 9) and the tall herb meadow (loc. 10) was probably connected to the structure of the organic soil. After a lowering of the water table these soils became mull-like.

In mineral soils *Dendrobaena* spp. are confined to the uppermost horizons (litter, mor) or A_1 and have no connection with the amount of organic matter of the mineral horizons. Large numbers of *Dendrobaena* spp. were found in biotopes where the litter decomposition was slow, for instance in coniferous plantations or beech woods. In elm and elm-ash woods with great yearly variations in surface litter quantities, the number of *Dendrobaena* spp. was low and *L. castaneus* was the most abundant of the surface-living species.

Mineral-soil-living species are strong burrowers, that actively transport organic matter to a depth of 50–60 cm. This promotes the formation of humus (BORNEBUSCH 1930, GRAFF 1953, VAN DER DRIFT 1963). It is not possible to determine whether the correlations found between the amount of organic matter in the layer 20–60 cm and abundance of *L. terrestris*, *A. caliginosa*, *A. longa*, and *A. rosea* are due to a preference by the worms for mineral soils with high amounts of organic matter or if they are the result of their transport activity.

There are some indications that the correlations found may not indicate any true relation. Mineral soils with a high content of clay as a rule show a higher loss on ignition and after correlation a higher amount of organic matter than do soils with a low content of clay. The correction factor used for weight loss due to constituent water (EKSTRÖM 1927, HOWARD 1966) may be too rough. HOWARD (1966) pointed out the likelihood of over-estimating the amount of organic matter at lower depth.

This study confirms the statement of STÖCKLI (1958) that the content of organic matter affect the earthworm abundance "nur in weitem Rahmen".

5.3. Porosity

The mechanical action of earthworms causes increased soil porosity (Stöckli 1928, Evans 1948, Baver 1956). Van Rhee (1969) found that the percentage of larger capillary pores was increased as a result of earthworm activity.

Organic soils had a high water capacity at low pF-values, i. e. a great porosity (table 2). In mineral soils the porosity decreased with increasing depth. Generally, B and C horizons were highly consolidated. The total volume of capillary pores with the diameter 2–2000 μm (fine, medium, coarse) and 200–2000 μm (coarse) was greater in sandy soils than in clayey (table 2).

There were no significant correlations between porosity and total abundance or biomass of earthworms. In clayey soils ($n = 7$) the porosity (20–60 cm) was greater at higher numbers of deep-burrowing earthworms ($r = 0.81$; $0.05 > P > 0.01$).

The distribution of pores depends among other things on the textural composition of the soil. For that reason no correlation between earthworms and volume of capillary pores can be proved when texturally different soils are compared. In this study no correlation could be found even when similar soils were compared.

It is possible that a correlation could be demonstrated between volume of capillary pores and abundance of earthworms, particularly that of deep-burrowing species of a study was carried out on a homogeneous soil. Figures of estimated standard deviation (Andersson 1970) indicate that more samples should be taken. Even if an evident correlation could be found it would be difficult to separate pores due to the action of worms from those caused by tjaele and roots. The co-operation between roots and worms has been pointed out by Rogers and Head (1968).

5.4. Water permeability

Hopp and Slater (1948) found that water entered the soil three to four times faster when soil was inoculated with living earthworms. Guild (1955) calculated the increased drainage due to earthworm activity to four times.

Sandy soils had a high vertical water permeability (table 2). High k-values were obtained in the A horizon, even in soils where silt and clay fractions were considerable. The high clay content in the layer 40–60 cm in soils of Baltic moraine (locs 12, 15, 16, 17) caused a low permeability. Pore volumes were here estimated to be 35–40 % and the volume of capillary pores constituted 3–7 %.

Water permeability depends on the texture and structure of the soil. The amount of capillary pores was high in sandy soils (table 2). Texturally dependent pores were more frequent in soils dominated by finer fractions and highly consolidated. The low permeability in these soils was caused by the few structurally dependent pores. Water permeability is proportional to the fourth power of the pore radius, i. e. a capillary of a certain size implies

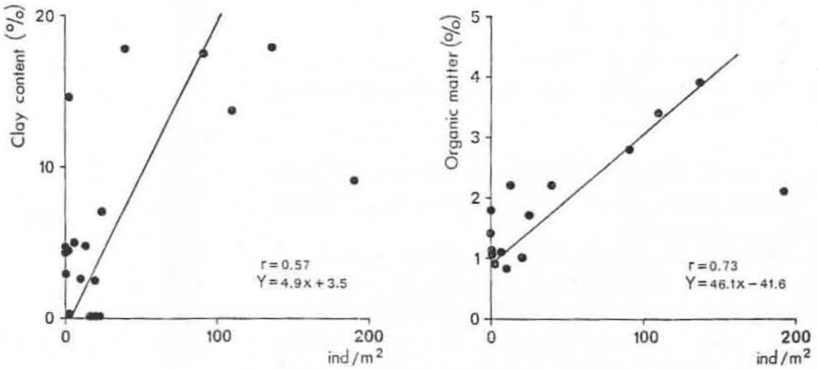

Fig. 4. Relationship between abundance of deep-burrowing earthworms and clay content (0–60 cm) (left) and organic matter (20–60 cm) (right).

the same permeability as 10,000 pores one tenth the size (ANDERSSON 1953a). That means that earthworm burrows, root channels or fissures are of great importance to the water permeability in clayey soils. There is no relationship between total porosity and permeability (ANDERSSON 1953a). Permeability is strongly correlated to the amount of coarse pores.

No significant correlation was found between k_v-values and earthworm abundance. The variable genesis and formation of the pore system in various soils made a decisive result impossible. A study of the importance of earthworm activity to permeability must be carried out in soils with the same textural composition.

5.5. *p*H

Lumbricids occur in acid as well as neutral soils (BORNEBUSCH 1930, ZUCK 1952, SATCHELL 1955, BALTZER 1956). Various species exhibit different responses to the concentration of hydrogen ions (LAVERACK 1961), and this may be important for the composition of lumbricid associations.

The classification given below is based on average *p*H values (0—60 cm) and does not take into account the various genesis of the soils.

1. Acid soils, *p*H 3.5—4.2: coniferous plantations (locs 1, 2, 3, 8, 11) and beech wood (loc. 4).
2. Acid — weakly acid soils, *p*H 4.2—5.5: woods (locs 5, 9, 20) and meadow (loc. 10) on organic soils, Juniperus pasture (loc. 13), spruce plantation (loc. 16) and beech wood (loc. 17).
3. Weakly acid — neutral soils, *p*H 5.5—6.6: open land (locs 6, 7, 19) and deciduous woods (locs 12, 15, 18).

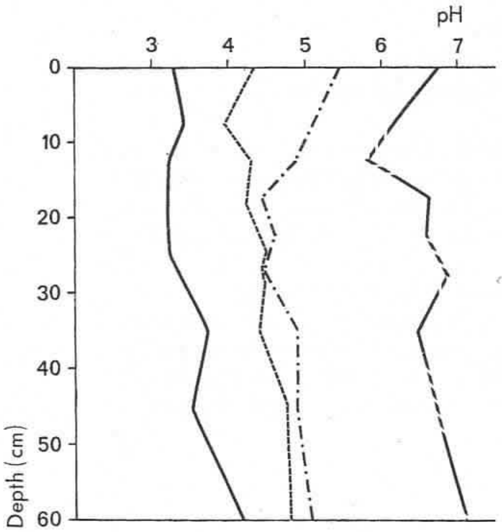

Fig. 5. *p*H variation with depth, from left to right, in pine plantation (loc. 11), alder-pine wood (loc. 5), beech wood (loc. 17), and elm-ash wood (loc. 15).

Low *p*H values and a negative *p*H gradient (LINNERMARK 1960) were found in podsoloids with coniferous plantations (fig. 5, table 2). The beech wood (loc. 4) with a mesotrophic brown forest soil on glacifluvial deposits had low *p*H values.

*p*H showed a slight vertical variation in organic soils. Highest values (*p*H 5.0—5.5) were obtained in the alder-birch wood (loc. 9) and the tall herb meadow (loc. 10). The 40-year-old spruce plantation (loc. 16) (first generation) had previously a brown forest soil. Higher *p*H values were still recorded here than in the other coniferous biotopes. The podsolisation process is retarded due to the clayey soil rich in basic material. Leaching processes were more pronounced in the Juniperus pasture (loc. 13) than in the adjacent elm-ash wood

(loc. 12). The brown forest soil in the beech wood (loc. 17) on Baltic moraine had higher pH than that on glacifluvial sand (loc. 4).

Manure and fertilizers were applied to the permanent pasture (loc. 7) until 1963. The high pH values at depths below 40 cm in the sand-dominated soil of the abandoned grassland (loc. 6) was due to the influence of Lake Krankesjön (pH 7.8). Soils on Corynephorus heaths are weakly acid (see Sjörs 1956). In deciduous woods (locs 12, 15, 18) the eutrophic brown forest soil had pH values generally above 6.0.

A significant correlation existed between pH (0–60 cm) and biomass ($r = 0.61$; $0.01 > P > 0.001$) but not between pH (0–60 cm) and total abundance ($r = 0.44$; $0.1 > P > 0.05$). A higher average weight per specimen was found when pH (0–60 cm) increased

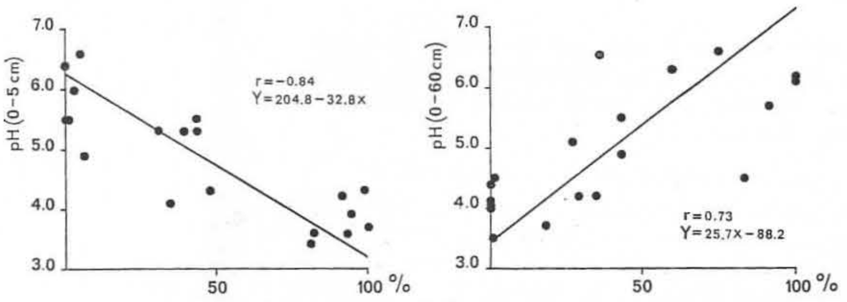

Fig. 6. Relationship between dominance values of *Dendrobaena* spp. and pH (0–5 cm) (left) and dominance values of deep-burrowing species and pH (0–60 cm) (right).

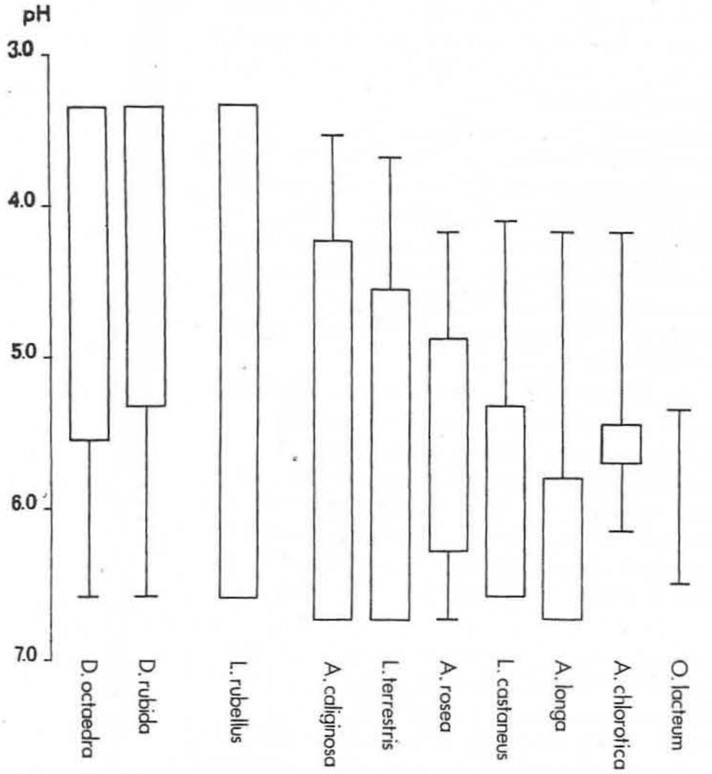

Fig. 7. Classification of earthworm species according to pH. Three groups can be distinguished: acidophilic, indifferent, and acidophobic species. Column = > ind./m², solid line = < 5 ind./m².

($r = 0.64$; $0.01 > P > 0.001$). Average weight per specimen was at *p*H 4.0 half of that at *p*H 6.0.

Dendrobaena spp. dominated in soils with low *p*H (0–5 cm) ($r = -0.84$; $P < 0.001$) (fig. 6). The correlation between *p*H (0–5 cm) and abundance of *D. octaedra* and *L. castaneus* respectively, were significant ($r = -0.55$ and $r = 0.51$; both $0.05 > P > 0.01$).

L. rubellus was abundant both in neutral soils as in the elm-ash wood (loc. 15) with *p*H (0–20 cm) 6.3 and in acid soils as in the pine plantation (loc. 11) with *p*H (0–20 cm) 3.3. There was no significant correlation between *p*H and abundance of this species ($r = 0.03$).

Dominance values of deep-burrowing species as well as total abundance were higher in weakly acid – neutral soils than in acid ($r = 0.73$; $P < 0.001$ and $r = 0.60$; $0.01 > P > 0.001$) (fig. 6). The abundance of *A. rosea*, *A. caliginosa*, *A. longa* and *L. terrestris* showed a significant correlation with *p*H (0–60 cm) ($r = 0.50$, $r = 0.55$, $r = 0.54$, $r = 0.57$; all $0.05 > P > 0.01$).

The number of species was significantly correlated with *p*H (0–60 cm) ($r = 0.47$; $0.05 > P > 0.01$). The most striking exceptions were (1) the Corynephorus heath (loc. 19) with only two species and *p*H ranging from 5.5–6.5 in the profile and (2) the alder wood (loc. 20) with ten species and a *p*H variation from 4.0–4.3.

Regarding relations to *p*H the species could be classified into three groups (fig. 7):

1. Acidophilic species: *D. octaedra* and *D. rubida*. The abundance decreased at higher *p*H.
2. Indifferent species: *L. rubellus*. This species occurred in > 5 ind./m^2 from *p*H 3.3 to 6.6.
3. Acidophobic species: *A. rosea*, *A. caliginosa*, *A. longa*, *A. chlorotica*, *L. terrestris*, *L. castaneus* and *O. lacteum*. The abundance decreased at lower *p*H. Except for *A. caliginosa* and *L. terrestris* the acidophobic species were absent at *p*H < 4.0.

*p*H differences between litter and mineral soil could be considerable. Occurrence and abundance of a species were therefore correlated with *p*H of the layer which it normally inhabits. Surface living species in particular ought to be independent of direct influences from *p*H of horizons underlying litter and mor. In the same biotope both acidophilic and acidophobic species exist simultaneously (see SATCHELL 1955).

The classification of lumbricids according to the acidity of the soil is similar to that of SATCHELL 1955). *D. octaedra* was, however, not restricted to biotopes with low *p*H. Even at *p*H 5.5 this species was abundant, but at higher *p*H the abundance decreased. If this was caused by high *p*H or other factors e. g. changes in food supply or interspecific competition was obscure. SATCHELL (1955) found *D. rubida* to be acid tolerant and to have the most narrow amplitude with regard to *p*H and *D. subrubicunda* to be ubiquitous. But in our materal *D. rubida* was not split into subspecies, i. e. *D. rubida* (SAV.) f. *typica* and *D. rubida* (SAV.) f. *subrubicunda* (EISEN) (see GERARD 1964); and wide amplitude found may depend on differences in habitat selection of the two subspecies.

In soils with low *p*H deep-burrowing species are unimportant and are replaced by surface dwellers. SATCHELL (1955) found significant positive correlations between *p*H and the numbers of *A. caliginosa*, *A. rosea*, *L. terrestris*, and *L. castaneus*. These observations are confirmed by the present study, where *A. longa* was significantly and positively correlated with *p*H. It has a more restricted amplitude with regard to *p*H than *A. caliginosa*. They always occurred together. However, *A. caliginosa* was found in small numbers in four more biotopes, all with low *p*H. The distribution of this species in Vomb may be a result of recent changes in the biotopes from former arable land to coniferous plantation, or by dispersion from adjacent biotopes.

Laboratory experiments on *L. rubellus*, *L. terrestris*, and *A. longa* (LAVERACK 1961) have shown a good correspondence with field observations on the distribution of these species. Of the species studied *A. longa* responded more negatively to low *p*H than did *L. rubellus*. Because of his own and LAVERACK's findings SATCHELL (1967) was of the opinion that "the distribution of earthworms in relation to mull and moor appears to be controlled by their response to the *p*H of their environment". The present study demonstrates strong correla-

tions between pH and the distribution of lumbricids. These may depend on pH directly or on factors connected with pH such as vegetation and food.

5.6. Soil moisture

Stöckli (1928) stated that occurrence and abundance of lumbricids primarily depend on soil moisture. Low soil moisture content is lethal to lumbricids (Grant 1955, Baltzer 1956, Zicsi 1959) and is often in the field combined with high soil temperatures. The effects of these two factors may therefore be difficult to separate and obtained results hard to interpret.

Regarding soil moisture the biotopes could be brought together in four main groups:

A. Soil moisture varying between maximal water capacity and pF 2.0: alder-pine wood (loc. 5) on organic soil.

B. Soil moisture around pF 2.0, pF > 3.2 never recorded: locs 1, 4, 8, 9, 10, 13, 17, 18, and 20 (fig. 8).

C. Soil moisture normally between pF 2.0 and 3.2. pF 3.2 to 4.2 were recorded temporarily and always superficially at locs 6, 11, 12, and 15, and frequently during summer in the uppermost 20 cm on the permanent pasture (loc. 7; fig. 8). Maximally a pF-value of 3.85 was recorded in the uppermost 5 cm (loc. 7) and the average value in the layer 0–5 cm was pF 3.35 from June to August.

D. Soil moisture mainly between pF 2.0 and 4.2. pF 4.95 recorded at driest occasion in the 0–5 cm layer during early summer on the Corynephorus heath (loc. 19). pF > 4.2 recorded during short periods in October in spruce plantations (locs 2, 3). A long drought affecting deeper layers was prevailing in the spruce plantation (loc. 16) (fig. 8).

No significant correlation could be shown between soil moisture (average June–August or driest time of sampling) expressed in pF-values and abundance or biomass of earthworms.

The variation of abundance in groups B and C was considerable (fig. 9). The biotopes in group B had 68.1 ind/m^2 as an average and those in group C 115.5 ind/m^2. The average abundance of the four biotopes in group D was only 20.3 ind/m^2. There was a significant difference between the average number of earthworms in the BC groups on the one hand and that of the D group on the other ($0.01 > P > 0.001$). The abundance was low in biotopes with low yearly content of soil moisture.

Expressions describing the retention of water are more ecologically adequate than are those giving weight or volume percentage of water. The amount of water available to an organism differs considerably in various soils depending on the structural and textural properties (see Nordström and Rundgren 1972, figs. 5, 9). Values of percentage give no information of the availability.

Kühnelt (1960) divided soils into three biologically distinct groups: Grundwasserböden – which are always saturated with water, Feuchluftböden – in which pF > 3.9 is never exceeded, and Trockenluftböden – in which pF 4.0 is reached. pF 4.0 is an important limit, as the relative humidity of the soil air at this value is < 100 % (see Schofield 1935). These three groups correspond roughly to groups A, BC, and D mentioned above.

Evidently, most soils in the investigated area normally have a soil moisture content sufficient for lumbricids. Biotopes where pF-values > 4.2 were recorded, had lower average abundance than those with pF-values < 4.2. Nielsen (1959) stated the limit of available water to the soil fauna to be pF 4.15–4.50. Gerard (1967) showed that only a few lumbricids could survive a long dry period with pF-values above 4.28. Zicsi (1959) has pointed out the effects of drought on lumbricids abundance and on population recovery time in natural biotopes.

Prevailing soil moisture in a biotope may influence the species complex. Some species may be excluded because of too low soil moisture. Low soil moisture content in combination with high surface temperatures on the Corynephorus heath (loc. 19) produces unfavourable conditions for surface-living species. The two species inhabiting this biotope, *A. caliginosa* and *A. longa*, are strong burrowers and can escape the rigours of drought and heat. Furthermore, both species undergo diapause during unfavourable soil conditions (Evans and Guild

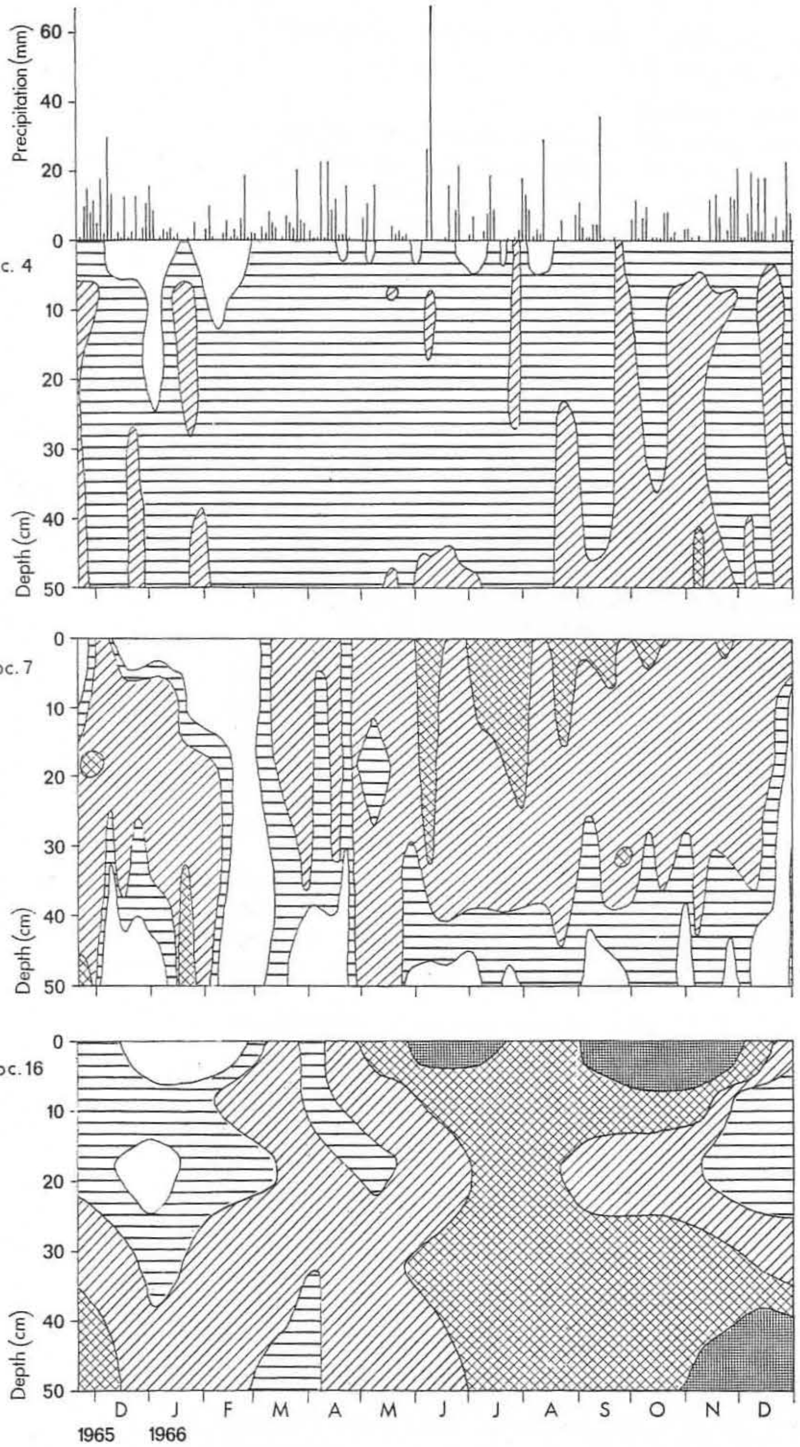

Fig. 8. Soil moisture variations in beech wood (loc. 4), permanent pasture (loc. 7), and spruce plantation (loc. 16) during Nov. 1965 to Dec. 1966. Precipitation at Björka expressed as 2-day values. Blank area = pF < 1.0, horizontally hatched = pF 1.0–2.0, diagonally hatched = pF 2.0–3.2, diagonally cross-hatched = pF 3.2–4.2 and cross-hatched = pF > 4.2.

1947). The absence of *L. terrestris* which has no diapause (EVANS and GUILD 1947, GERARD 1967) from the Corynephorus heath may be due to the extreme environment.

Low constancy of surface-living species on permanent pasture has been discussed (see NORDSTRÖM and RUNDGREN 1973, table 10). The effect of low soil moisture content in combination with high soil surface temperatures may influence the lumbricid association in such biotopes. At loc. 7, pF-values > 3.2 were recorded on 9 out of 13 sample occasions during the summer 1966 in the 0—5 cm layer. This implies that especially surface-living earthworms would be exposed to long periods of drought close to the lethal limit.

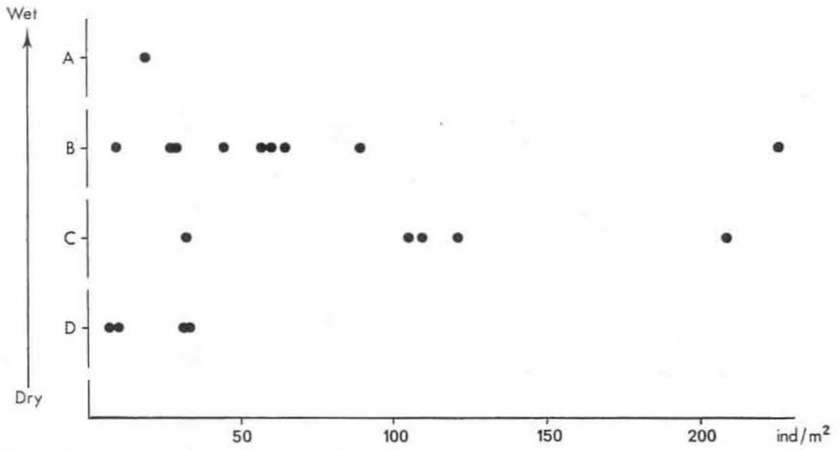

Fig. 9. Total abundance of earthworms in relation to yearly soil moisture conditions. A = soil moisture varying between maximal water capacity and pF 2.0, B = soil moisture around pF 2.0, pF > 3.2 never recorded, C = soil moisture normally between pF 2.0 and 3.2, D = soil moisture mainly between pF 2.0 and 4.2.

Due to high interception (STÅLFELT 1960, NIHLGÅRD 1970) all spruce plantations except for the youngest one (loc. 1) had low soil moisture content. Great differences of moisture in litter and mor occur due to low stem flow (NIHLGÅRD 1970), variable throughfall (STÅLFELT 1960), patchy bottom layer and varying thickness of surface litter. Soil temperatures recorded were lower than those on the permanent pasture and on the Corynephorus heath. In spruce plantations soil moisture conditions in the true soil do not exclude a *Dendrobaena* octaedra association.

It has been assumed that *A. chlorotica* is bound to biotopes with high soil moisture content (ZUCK 1952, BALTZER 1955, 1956). During 1966 this species was found in seven biotopes in the Vomb Depression, all belonging to the groups B and C (approx. „Feuchluftböden"). The low soil moisture content on the permanent pasture was, however, not sufficient to exclude this species. *A. chlorotica* is a deep burrower and can by inactivity survive summer droughts.

Presumably the effect of low soil moisture is most important to activity (EVANS and GUILD 1947, GERARD 1967) and to the survival of cocoons and of juveniles hatched during spring (GERARD 1967). Juveniles as well as surface-living species are exposed to great variations in soil conditions as regards moisture and temperature at the surface which affect the structure of the population.

5.7. Soil temperature

Climatically southern Sweden is situated in a zone where soil temperature at winter and summer, especially at the soil surface, generally surpass temperatures constituting the limits of motor activity in lumbricids. This means that twice a year there occur unfavourable conditions leading to quiescense (diapause) in some species (see EVANS and GUILD 1947, GERARD 1967, SATCHELL 1967). Soil temperature, by influencing activity, may also affect numbers and species complex of earthworms.

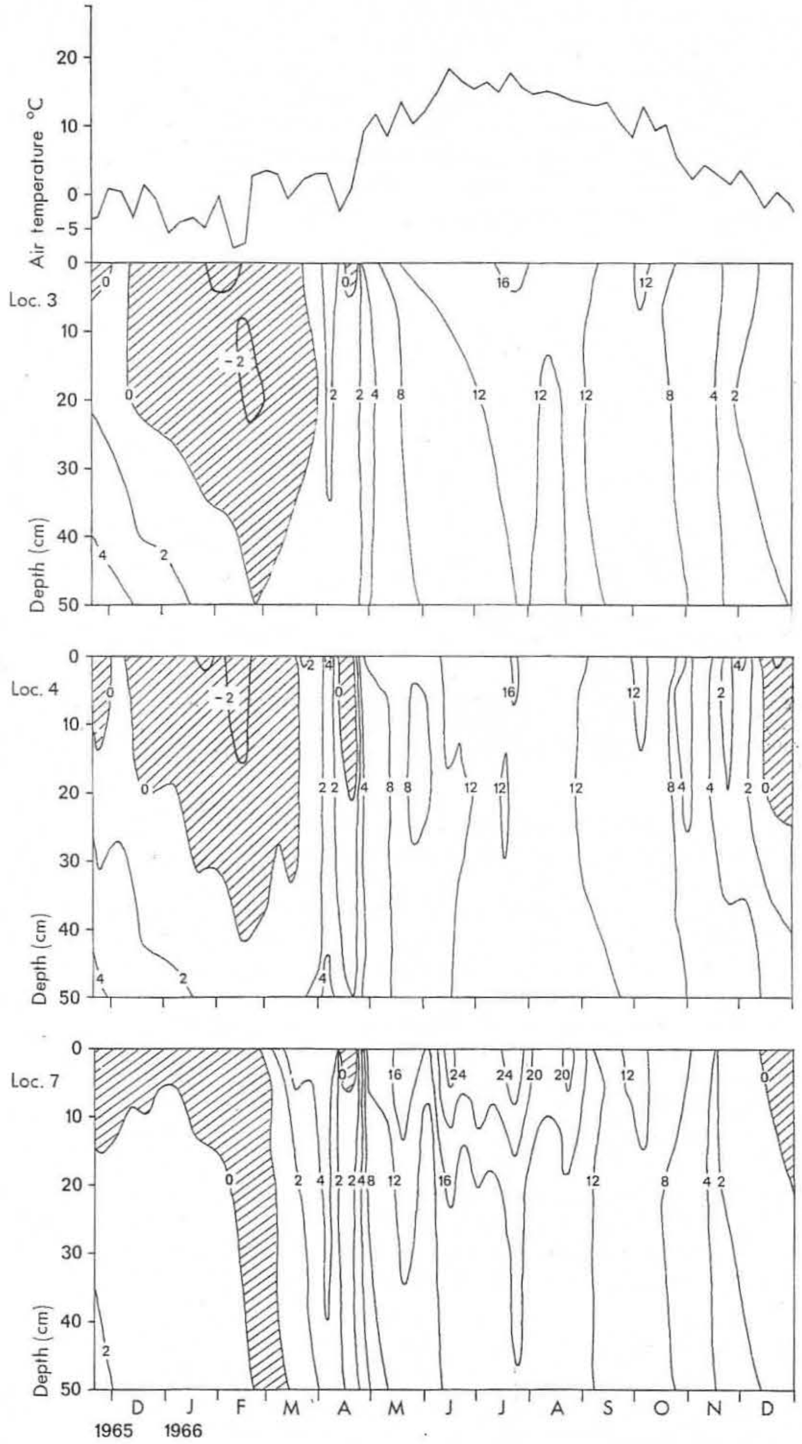

Fig. 10. Air temperature at Björka and soil temperatures in spruce plantation (loc. 3), beech wood (loc. 4), and permanent pasture (loc. 7) during Nov. 1965 to Dec 1966. Diagonally hatched area = temperatures below 0 °C, with −2 °C indicated.

The course of the yearly soil temperatures showed great similarity in various biotopes (fig. 10). Some differences occurred between coniferous and deciduous woods at the lowering of temperature in autumn and the warming up in spring. This was most pronounced before leafburst, but also due to variations in snow cover (thickness and lasting) in early spring.

A temperature deficit compared with average values during 1901—1930 prevailed during the winter 1965—1966 and the total time with mean temperatures below 0 °C was longer than normal. Soil temperatures below 0 °C were recorded in all biotopes in the uppermost layers during winter and the soil was frozen (fig. 11). The depth of tjaele was greatest in exposed biotopes. Also in spruce plantations the depth of tjaele was considerable, whereas deciduous woods which had greater snow-cover did not freeze to the same depths. Striking differences occurred between the two parts of the pine plantation (loc. 8). The tjaele at soil surface lasted longer in exposed biotopes. The soil of the Corynephorus heath (loc. 19) was

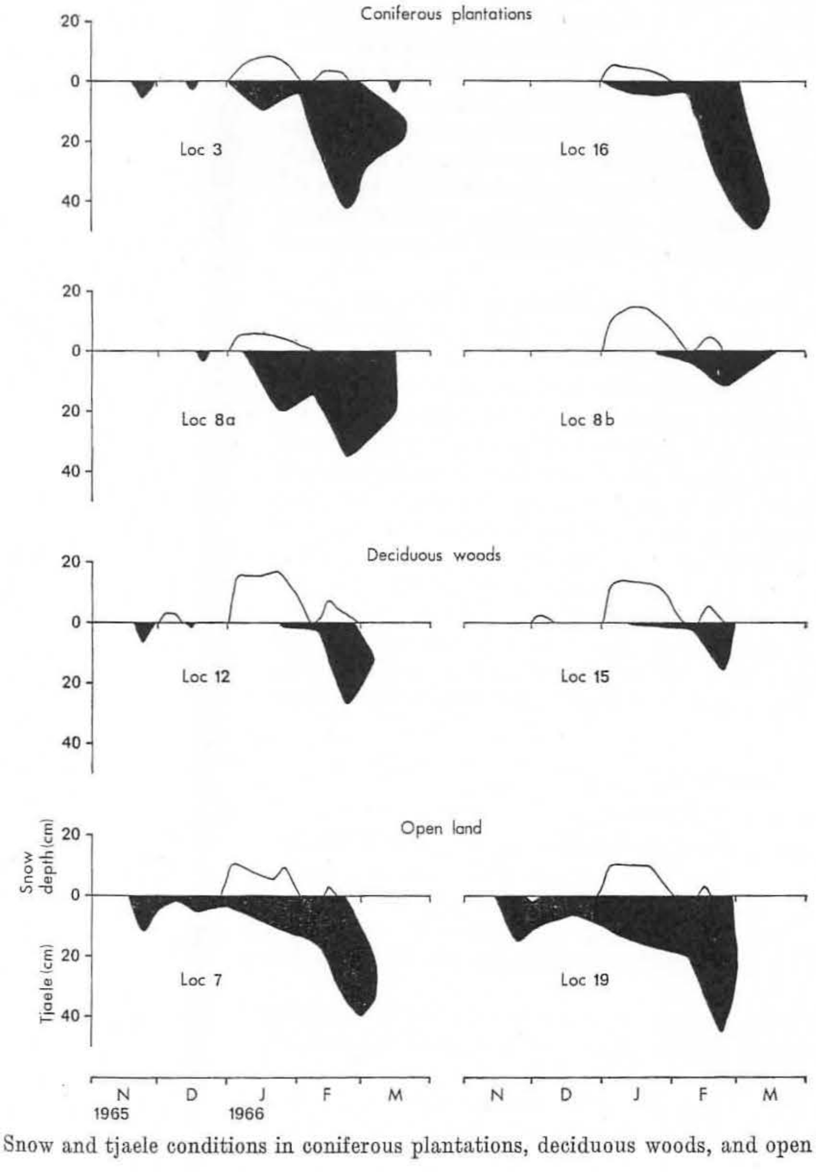

Fig. 11. Snow and tjaele conditions in coniferous plantations, deciduous woods, and open land.

frozen for 110 days; the elm-ash wood (loc. 15) for only 45 days. At depths below 20 cm tjaele existed longer in biotopes where the warming up was slow.

In no wooded biotope were soil temperatures above 20.0 °C recorded during summer, not even on the warmest day (22 July) with a maximum daily air temperature of 28.0 °C (SMHI 1965—1967). Highest temperature recorded at soil surface (—1 cm) was 27.0 °C on the pasture (loc. 7) and 27.8 °C on the Corynephorus heath (loc. 19).

Hopp and Linder (1947) as well as Barley (1961) reported that lumbricids die when temperature falls below 0 °C. The severe winters in the 1940's in Denmark radically but not completely decreased the numbers of earthworms (Larsen 1949). From figures obtained in September—November 1966 (table 1) the effect of low temperatures on abundance cannot be elucidated, but samples in spring showed a decrease in numbers due to soil conditions during winter. In no biotope could a complete disappearance due to frost be proved.

Species distribution seems to be unaffected by low soil temperatures. Surface-living species, which are exposed to large temperature variations and are repeatedly frozen, were found in the tall herb meadow (loc. 10) but not on the Corynephorus heath (loc. 19). In these biotopes soil temperatures during winter as well as duration and depth of tjaele were comparable. It is reported that *D. octaedra* in order to avoid low temperatures penetrates to deeper layers (Bornebusch 1953). This was not supported in this study. In March 1966 when the tjaele was 25 cm, this species was found exclusively in the layer 0—5 cm in the spruce plantation (loc. 3). Low temperatures in combination with tjaele had no effect on the distribution of deep-burrowing species. *Allolobophora* spp. were found in exposed biotopes (locs 13, 19) with deep and lasting tjaele, but was absent from less exposed biotopes. The distribution of *L. terrestris* were also barely influenced by tjaele and low temperatures. These species are able to avoid low temperatures by burrowing.

Wolf (1938) determined the lethal temperature of *L. terrestris* to be 28.0 °C for an exposure of 400 min. This figure is close to the thermal death point found by Hogben and Kirk (1944). The lethal temperature of *A. longa* was determined to be 25.7 °C by Miles (1963). Temperatures of this magnitude were measured in five biotopes and may have reduced the abundance of lumbricids (see Nordström and Rundgren 1972, tables 1, 3).

Biotopes where high soil-surface temperature in combination with low soil moisture content may influence the species complex were the pasture (loc. 7) and the Corynephorus heath (loc. 19). In these biotopes high temperatures (above 25.0 °C) were sometimes recorded down to a depth of 5 cm. Such figures, normal in summers in these biotopes, may decrease the possibilities of surface-living species to establish a population. Temperatures above 25.0 °C at soil surface (—1 cm) were also recorded in other biotopes (locs 1, 6, 10). The high soil temperature in the young spruce plantation (loc. 1) was only temporary due to shading effects from trees and bushes. On the abandoned grassland (loc. 6) and the tall herb meadow (loc. 10) high temperatures were not combined with low soil moisture. These biotopes were assigned to "Feuchtluftböden" and soil moisture was always available to the surface-living species.

5.8. Vegetation

5.8.1. *Birch versus pine*

The pine part (8a) and the birch strips (8b) in the pine plantation did not differ significantly as to total abundance and species complex. *D. octaedra* was the dominating species in both areas and no difference in abundance could be shown to exist. *A. caliginosa* and *D. rubida* occurred sparsely. The numbers of *L. terrestris* were, however, significantly higher in the birch strips ($P < 0.001$). As a consequence, the biomass was higher in this part ($0.01 > P > 0.001$).

Former land-use was similar in the two areas. No difference was found as regards texture, porosity and water permeability or in amount of organic matter in the mineral soil and *p*H. Retention of water and yearly soil moisture regime were similar. Some differences were found in the microclimate, the birch part was more exposed and had a deeper tjaele (fig. 11). But this can hardly explain the differences found in abundance of *L. terrestris* and in total biomass.

The composition of the surface litter was obviously different. In the pine part it consisted only of pine matter. In the other part birch leaves and matter from a rich field layer were also present. Regarding *D. octaedra* the quality of food seems to be equivalent in both areas of the pine plantation. As the species does not feed on newly fallen needles of pine or spruce (LINDQUIST 1941) it probably feeds on decomposed litter, humus (BORNEBUSCH 1953) or on organisms associated with decomposition processes. *L. terrestris* feeds on litter transported downwards. Birch leaves are not highly preferred, but the species feeds on this as well as on litter from the field layer (LINDQUIST 1941, BORNEBUSCH 1953, SATCHELL and LOWE 1967). The difference in abundance of *L. terrestris* between the two areas of the biotope seems to be due to dissimilarities in litter composition.

5.8.2. *Succession in coniferous plantations*

There was no significant difference between the two young spruce plantations (locs 1, 2) regarding abundance and biomass of earthworms (fig. 12). *D. octaedra* was the dominating species, but not overwhelmingly so in the youngest one. The old spruce plantation (loc. 3) had a higher total abundance and biomass than any of the other two ($0.01 > P > 0.001$). *D. octaedra* dominated in both pine plantations (locs 8a, 11). The abundance was lower in the younger one ($P < 0.001$) (fig. 12), as were total abundance and biomass ($P < 0.001$ and $0.01 > P > 0.001$, respectively).

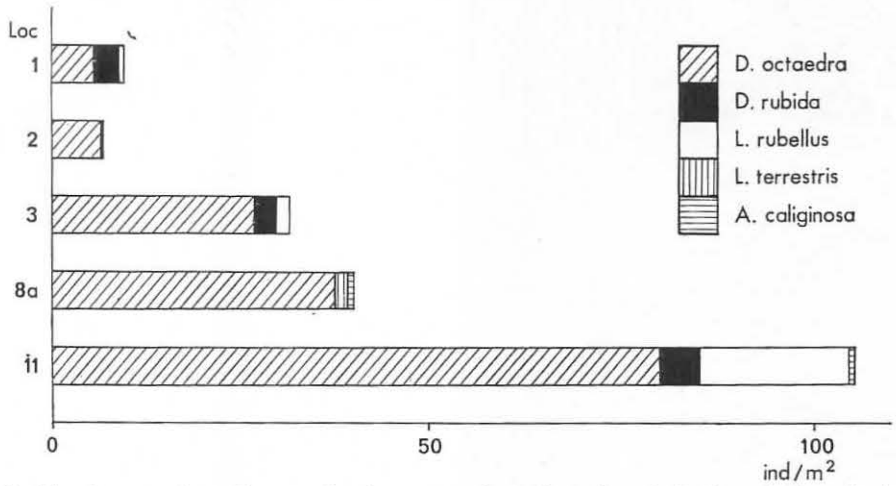

Fig. 12. Abundance and species complex in spruce plantations (locs 1, 2, 3) and pine plantations (locs 8a, 11).

The three spruce biotopes were formerly subjected to different land-use. At the time of the investigation no clear differences were found between the biotopes with regard to soil texture, *p*H or water retention that could explain the differences in abundance and biomass found. The youngest spruce plantation had a higher amount of organic matter in the uppermost 20 cm reflecting its former use as a pasture. It also had a better soil moisture regime and was assigned to "Feuchtluftböden". It differed also slightly as to microclimate. This biotope was more exposed as the canopy was not quite closed.

The supply of decomposed litter as well as the degree of decomposition of the litter matter differed in the biotopes. In the 12-year-old plantation no mor horizon had developed. The 25-year-old spruce plantation had a 0.5 cm thick mor horizon and the 45-year-old plantation a 2—3 cm thick one. In the young pine plantation no mor horizon was developed and the thickness of litter varied between 1—7 cm. Before planting the pasture at that time had been ploughed and litter had accumulated in the furrows still recognizable, while the litter layer on plough-beams was thin (fig. 13). The litter was more evenly distributed in the old

pine plantation, varying between 2–3 cm. In this biotope a thin mor horizon (< 1 cm) had developed.

It seems that the quality of litter, e. g. the degree to which the litter has been decomposed, is important for the abundance of *D. octaedra*.

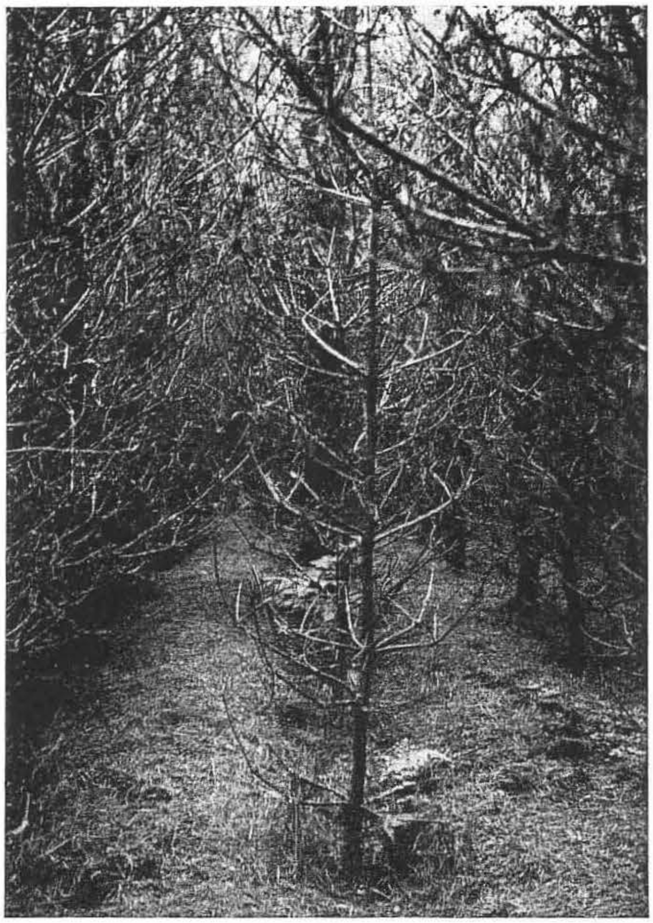

Fig. 13. Pine plantation (loc. 8 a). The area, a former pasture, was ploughed before planting. Litter has accumulated in the furrows while litter layer on plough-beams is thin.

5.8.3. *Alterations of a grazed open woodland*

The elm-ash wood (loc. 15), the spruce plantation (loc. 16) and the beech wood (loc. 17) grew on land subjected to extensive grazing until ca 1900. Identical influences by man and a similar vegetation on similar substratum indicate that there had previously been a rather uniform lumbricid fauna in this area. In the 1920's spruce was planted in the middle part separating the earlier open woodland in two parts, of which one was left developing an elm-ash wood and the other by management became a beech wood.

In the elm-ash wood nine lumbricid species occurred and in the beech wood eight (table 1). The species complex was identical in these two biotopes except for *O. cyaneum* occurring in the elm-ash wood. The spruce plantation had four species. Total abundance in the two deciduous woods did not differ significantly ($0.1 > P > 0.05$), whereas the spruce plantation had considerably lower abundance ($P < 0.001$). The elm-ash wood had higher biomass than

the beech wood (0.01 > P > 0.001) as the large deep-burrowing species dominated. In the spruce plantation the biomass was significantly lower than in the deciduous woods (P < 0.001) due to dominance of surface-living species and lower total abundance. There were no significant differences in abundance of surface-living species between the three biotopes. In the spruce plantation these were represented only by *Dendrobaena* spp. The abundance of *D. octaedra* was lowest in the elm-ash wood (P < 0.001). *L. castaneus* occurred in the two deciduous woods. The abundance of deep-burrowing species was in the order elm-ash wood > beech wood > spruce plantation (P < 0.001). *A. caliginosa* was the only deep-burrowing species found in the spruce plantation. Its numbers there were significantly lower than in any of the deciduous woods (P < 0.001). The numbers of *A. longa* and of *L. terrestris* differed significantly between the elm-ash and the beech woods (0.01 > P > 0.001 and P < 0.001, respectively), but this was not the case with *A. rosea* and *A. caliginosa*.

The thickness of surface litter was rather constant in the spruce plantation, whereas it varied considerably in the deciduous woods during the year (fig. 14). Leaf litter was almost completely decomposed in the elm-ash wood at the beginning of following summer. Allochthonous beech leaves were still intact. The surface litter in the beech wood was compressed during winter under the influence of rain and snow. The decomposition was not completed in one year.

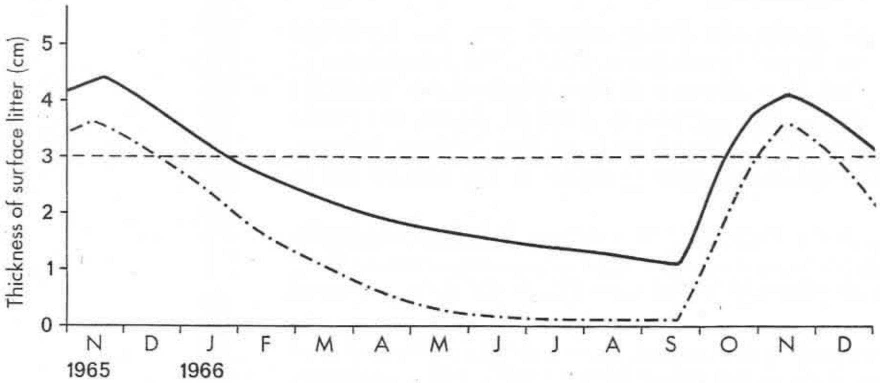

Fig. 14. Yearly variation in thickness of surface litter in spruce plantation (loc. 16, broken line), beech wood (loc. 17, unbroken line) and elm-ash wood (loc. 15, dotted broken line).

Dendrobaena spp. are poor burrowers bound to the superficial organic layers of the soil. Strong fluctuation in litter quantity and absence of mor in the elm-ash wood seemed to influence the abundance of *D. octaedra* negatively. Also in other elm-dominated woods (locs 12, 18) the same low abundance and dominance of *D. octaedra* occurred. This species was there replaced by *L. castaneus* which does not seem to be so extremely bound to organic layers. It also inhabits the uppermost mull horizon. Absence of *L. castaneus* in the spruce plantation cannot be explained by low *p*H alone. The other beech wood studied (loc. 4), with lower *p*H, contained *L. castaneus*. This biotope like most of the others where *L. castaneus* was found had a mull horizon, while the litter quality varied (grass, beech, alder, elm, ash).

Low *p*H, fluctuating water availability, and shortage of food were presumably critical factors for deep-burrowing species in the spruce plantation. The low abundance of these species in the beech wood compared with the elm-ash wood may be due to differences in litter quality, i. e. food.

Litter selection experiments have shown that most lumbricids have a higher preference for leaves of ash, elm and hazel than for leaves of beech (Lindquist 1941, Bornebusch 1953, Satchell and Lowe 1967). Furthermore, the palatable leaf litter in the elm-ash wood

was complemented by matter from a well-developed field layer containing among others *Mercurialis perennis* L., which is highly preferred by earthworms (LINDQUIST 1941, BORNEBUSCH 1953). Except for the vernal aspect the field layer was almost entirely absent in the beech wood.

Obviously, difference in litter quality is of minor importance to the abundance of *A. caliginosa* and *A. rosea* in the elm-ash and the beech woods. According to WATERS (1955) dead roots are an important food supply for *A. caliginosa*, while BARLEY (1959) and GRAFF (1964) suggested that this species feeds on micro-organisms. Unlike *A. caliginosa* and *A. rosea*, *L. terrestris* and *A. longa* are effective litter-decomposers (LINDQUIST 1941). The difference between the two deciduous woods in numbers of these two species may be related to litter quality.

Planting spruce radically changes the environment. The brown forest soil is subject to podsolization, an A_0 horizon develops, and pH decreases, especially in the uppermost layers. The mull aggregation disintegrates, the turn-over of litter is reduced, and organic matter is accumulated on the surface. The yearly soil moisture regime deteriorates. These changes affect the previous lumbricid association, which develops into a species-poor one, low in numbers and biomass and characterized by surface-living species.

6. Conclusion

In an earlier paper NORDSTRÖM and RUNDGREN (1973) showed that four lumbricid associations could be distinguished in the Vomb Depression in Skåne. The composition of these depends on certain environmental factors. Abundance and occurrence of some lumbricid species are related to clay content, organic matter, pH and, to a certain degree, the yearly soil moisture regime. Some of these factors are closely inter-related. For instance, biotopes with high clay content have also a high amount of organic matter in the mineral soil as well as a high pH.

A correlation found between coarse soil texture and low abundance may be incidental. Thus sandy areas are not used to the same extent as clayey areas as pastures or arable land. They are usually planted with spruce or pine with deleterious effects on the numbers of lumbricids.

An association is determined by a complex of co-operative factors as pH, vegetation, and food supply. But also other factors such as the yearly soil moisture regime, soil temperature and previous land-use (the historical aspect) may modify the association with regard to numbers, biomass or additional species of low dominance.

Two lumbricid associations in the Vomb Depression are related to distinct groups of biotopes. The other two are not so clearly defined.

The Dendrobaena octaedra association is bound to coniferous woods. Needle litter is unpalatable to most lumbricids. The soil is a podsol or a brown forest soil under podsolization, pH is low, and the yearly soil moisture regime shows deficits in available water. A brown forest soil under podsolization can in its first stages still maintain earthworms belonging to an earlier association.

The Allolobophora rosea — *A.* caliginosa — Lumbricus terrestris association belongs to pastures and deciduous woods dominated by ash or elm and with a well-developed field layer. Its litter is palatable to most lumbricids. The soil is a brown forest soil or a cultivated one, pH is almost neutral, and soil moisture is adequate.

The Allolobophora caliginosa — A. longa association seems to be a modified Allolobophora rosea — A. caliginosa — Lumbricus terrestris association, where some species cannot exist due to, among other things low soil moisture, high soil temperatures, and inadequate food supply.

The Dendrobaena octaedra — Lumbricus rubellus association is found in various biotopes. Vegetation, litter conditions, soil types and pH are highly variable. The association seems to form a transitional association between the two more extreme ones, the Dendro-

baena octaedra- and the Allolobophora rosea — A. caliginosa — Lumbricus terrestris associations respectively.

7. Summary · Rezjume

Lumbricid associations and their relationships to certain environmental factors were studied. Significant correlations between clay content as well as organic matter and abundance of deep-burrowing species were found. No significant correlation could be proved between porosity or water permeability and lumbricid numbers. *Dendrobaena* spp. dominated in acid soils and deep-burrowing species in weakly acid to neutral soils. All soils normally had a soil moisture sufficient for lumbricids. A few biotopes with temporarily low water availability had lower total abundance. Low soil temperatures during winter and the occurrence of tjaele did not eradicate the lumbricids. Surface-living species were absent in some exposed biotopes with high soil-surface temperatures. Significant differences were found in habitat selection of various species. It was suggested that these were mainly due to differences in litter quality.

The combination of *p*H, vegetation, and food seemed to determine the lumbricid association. The D. octaedra association was found in coniferous plantations with needle litter and low *p*H; the A. rosea — A. caliginosa — L. terrestris association in pastures and rich deciduous woods with palatable litter and high *p*H. The A. caliginosa — A. longa association seemed to be a modification of the latter and the D. octaedra — L. rubellus association transitional between the two main types.

[Факторы среды и сообщества дождевых червей в Южной Швеции]

Исследованы сообщества дождевых червей и их отношение к некоторым факторам среды. Установлены определенные корреляции между содержанием глинистых частиц и органического вещества и обилием видов, прокладывающих ходы в глубоких слоях почвы. Не найдены корр, еляции между количеством червей и порозностью либо влагоемкостью почвы. *Dendroraena spp.* доминируют в кислых почвах; они — обитатели глубоких горизонтов в лсабокислых и нейтральных почвах. Все обследованные почвы, как правило, имеют влажность, благоприятную ялд дождевых червей. В некоторых биотопах, где почва временно пересыхает, численность червей низкая. Низкие температуры зимой и временное промерзание не приносят вреда червям. Поверхностно живущие виды отсутствуют в некоторых открытых биотопах с высокой температурой поверхности почвы. Найдены существенные различия в выборе местообитаний у разных видов. Установлено, что они определяются преимущественно качеством подстилки. Состав комплексов дождевых червей определяется совокупностью таких факторов, как *p*H, растительность, запасы пищи. Популяции *D. octaetra* найдены в посадках хвойных пород с хвойным опадом и низкими значениями *p*H; комплексы *A. rosea — A. caliginosa—L. terrestris* обитают на постбищах и в богатых листопадных лесах со съедобной подстилкой и высоким *p*H; комплекс *A. caliginosa — A. longa* представляет очевидно модификацию предыдущей группы, а комплекс *D. octaedra — L. rubellus* занимает промежуточное положение между двумя основными типами.

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